Cold temperature tolerance and distribution of the brown recluse spider *Loxosceles reclusa* (Araneae, Sicariidae) in Illinois

Kenneth L. Cramer: Department of Biology, Monmouth College, 700 E. Broadway, Monmouth, Illinois 61462, USA. E-mail: kenc@monm.edu

Alex V. Maywright: Department of Biology, University of Missouri-St. Louis, R223 Research Bldg, One University Boulevard, St. Louis, Missouri 63121-4499, USA

Abstract. Although the temperatures at which the brown recluse spider (Loxosceles reclusa) is active have been described, no work has been done on lethal thermal limits that may influence the distribution of this medically important species. We tested the cold tolerance of L. reclusa at temperatures ranging from 3° C to -14° C. First, we tested spiders over brief 4-h exposures to a test temperature. Second, we tested spider tolerance to long-term, 30-da exposures to constant, low temperatures to simulate overwintering conditions. We also recorded temperatures beneath the plant litter layer and compared these to ambient surface air temperatures to estimate the effect of litter insulation. We then used the regression of ambient temperature to litter temperature to predict isotherms of litter retreats in Illinois during January, the month of lowest mean winter temperatures. Using the cold temperature lethal limits we found in the lab, we predicted a theoretical distribution of L. reclusa based solely on temperature that approximately matches its currently known distribution in Illinois.

Keywords: Biogeography, cold tolerance, lethal thermal limits, venomous spider, pest

The brown recluse spider, Loxosceles reclusa (Gertsch & Mulaik 1940), is distributed throughout the south-central United States (Gertsch & Ennik 1983; Vetter 2005). In its natural habitat, the brown recluse lives in dry, dark areas such as rocky overhangs, cliff ledges, bluffs, and under bark on dead trees. During winter months, L. reclusa can be found in silk retreats under stones on the ground (Hite et al. 1966). The brown recluse is also synanthropic, adapting to life in buildings as far north as Maine (McDaniel & Jennings 1983), though such outliers are rare and are the source of much misunderstanding (Vetter 2005). Because of the medical importance of the spider and confusion about its distribution in both the lay and medical communities (Vetter 2005), we investigated cold winter temperatures as one factor that could restrict the northern range of this species in Illinois, a state that spans the northern limits of its distribution.

Temperature acts as a barrier to the distribution of many animals but especially ectotherms such as spiders. Physiological and behavioral thermoregulation play a vital role in cold tolerance and, therefore, overwinter survival of spiders. Spiders vary greatly in resistance to cold temperatures with supercooling points (= SCP, the freezing point of hemolymph in an intact animal) ranging from -4° C to -34° C (Kirchner 1987). However, the temperature at which a spider can survive for periods of days is usually several degrees higher than the SCP. A variety of substances including proteins and polyhydric alcohols have been proposed as agents preventing icenucleation in the hemolymph (Husby & Zachariassen 1980; Zachariassen 1985; Kirchner 1987).

In winter, spiders regulate body temperature behaviorally by using leaf litter and accumulating snow as insulation from cold and variable ambient air temperatures. For instance, in Canada, a good snow cover can insulate the subnivean zone to temperatures no less than -9.5° C while the ambient air temperature plunges to -35° C, allowing for winter activity in

several families of spiders (Aitchison 1978). In addition, many spiders, including brown recluses, are known to spin silk retreats (Hite et al. 1966) that may have insulating properties.

Only two species of Loxosceles, both from South America, have been tested for cold temperature tolerance. Fischer & Vasconcellos-Neto (2003) found an LT₅₀ of -7° C for 1-h exposures in L. laeta (Nicolet 1849) and L. intermedia Mello-Leitão 1934. The brown recluse has never been tested for minimum lethal limits. We sought to determine the lethal minimum thermal limits of brown recluse spiders by exposing them to brief 4-hour or prolonged 30-da (= day) periods over a range of temperatures lower than 4° C, the point at which Hite et al. (1966) reported that they become inactive. We also recorded temperatures in the field in order to extrapolate temperatures beneath the leaf litter from ambient minimum air temperature isotherms for the state of Illinois. We chose Illinois as a model state to observe because its north-south axis straddles the northern boundaries of the range of L. reclusa reported in earlier literature (Gertsch & Ennik 1983; Vetter 2005). We then proposed a theoretical northern limit for the brown recluse based on their temperature tolerance and mean low winter temperatures beneath the litter layer.

METHODS

We collected brown recluses from a barn in the Little Creek Nature Preserve near St. Louis, Missouri (38.77419°N, 90.29150°W) and housed them individually in 5 × 5 × 3 cm clear plastic containers at room temperature (22° C) on a 12L:12D light cycle. Voucher specimens are deposited in the Biology Department at Monmouth College, Monmouth, IL. Spiders were acclimated to the lab environment for four weeks before testing began. We maintained spiders on house crickets (*Acheta domesticus* Linnaeus 1758) and did not initiate temperature tests until at least one week after their last feeding. From the sample population, we randomly designated

groups of 19–20 adult spiders to each treatment. We chose experimental temperatures based on information in Hite et al. (1966) and winter average low temperatures for 87 municipalities in Illinois having a continuous record from 1971–2000 available on the Illinois State Climatologist Office (2006) web site (http://www.sws.uiuc.edu/atmos/statecli/Summary/Illinois. htm).

Our first set of experiments tested *L. reclusa* at 4-h exposures. We placed each group of spiders in an incubator with relative humidity held constant at 30% (+/- 3%) and lowered the temperature by 4° C every 2 h from 22° C to the specified test temperature. Thus, spiders exposed to cooler temperatures underwent a longer cool-down period but all groups were cooled at the same rate. Humidity level was arbitrarily chosen but falls within the range of minimum humidity levels recorded in Illinois in winter months (Illinois State Climatologist Office, 2006). Spiders remained at the test temperature for 4 h and the temperature was then raised to 22° C in the same manner as it was lowered. We repeated this procedure for eight test temperatures: 3, 1.5, 0, -2, -5, -7, -10, and -14° C and recorded mortality rates.

In a second set of experiments we exposed spiders to low temperatures for 30 da to simulate overwintering conditions. Three different groups of spiders were gradually lowered as before in the 4-hour tests to 0, -2 and -5° C. After the 30-da period, the temperature was raised gradually, as in short-term experiments, to room temperature.

We analyzed the short-term temperature exposure mortality data using probit analysis (Minitab) to predict a lethal temperature for 50% of the test population (LT₅₀). Assuming a Weibull distribution gave the best fit of model to the data (P > 0.10, Hosmer-Lemeshow goodness-of-fit). The long-term temperature exposure data could not be analyzed by probit because, of the three temperatures tested, there were no mortalities at the highest temperature and no survivors at the lowest temperature. These zero values precluded the possibility of fitting a line with any accuracy.

Finally, in order to accurately predict microhabitat temperature in the leaf litter relative to ambient air temperature, we placed six Hobo temperature data loggers (Onset Computer Corporation) in LeSuer Nature Preserve near Monmouth, Illinois ($40.921036^{\circ}N$, $90.63101^{\circ}W$). For 16 wk from November 2003 to March 2004 we recorded temperatures to the nearest 0.4° C at 5-min intervals beneath the litter (O horizon) at the boundary with the A horizon (partially decomposed organic matter) in three locations and nearby with the same exposure but at the ground surface (n=3). We used mean daily values to calculate a regression between surface air and litter temperatures and used it in conjunction with mean minimum January air temperatures from the Illinois State Climatologist Office to produce a map of isotherms of litter temperatures across the state.

RESULTS

In the 4-h exposures to test temperatures (n=19 each treatment), there were no mortalities in any of the five groups of spiders tested at 3, 1.5, 0, -2 and -5° C. The -7° C and -10° C test groups each experienced 47% mortality and at -14° C mortality was 100%. Probit analysis predicts a short-term exposure LT₅₀ at -9° C (+/ -1° C) (Figure 1).

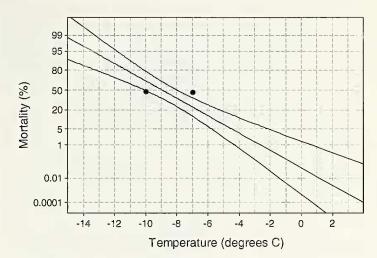


Figure 1.—Probability plot of mortality with 95% confidence intervals for 4-h exposures of brown recluse spiders at various temperatures. See text for details of data.

In the 30-da exposures (n=20 each treatment) all spiders held at 0° C survived, 30% survived at -2° and none survived at -5° C. Because of the zero values for mortality and survivorship in the high and low temperatures, respectively, probit analysis was not appropriate for these data. As expected, the long-term survivorship was greatly reduced compared to short-term exposures. Though we cannot estimate an LT₅₀ from these date, we can infer a long-term LT₁₀₀ of at least -5° C, possibly higher.

Over a 16-wk winter period (2003–2004), leaf litter temperatures averaged 3.0° C warmer than air temperature. The range of temperature fluctuation in leaf litter and air over the entire period was similar, about 15° C. Litter temperatures fluctuated up to 13° C in a 24 h period with episodes in November when the temperature dropped as much as 12° C in a 4-h period. The regression equation of litter temperature (Y) on air temperature (X) was Y = 1.87 + 0.65 (X), with $r^2 = 0.72$ (Figure 2).

We used our regression equation to estimate litter temperatures from air temperatures aeross Illinois and superimposed these isotherms over confirmed *L. reclusa* records across the state. Records included citizen's submissions to the principal

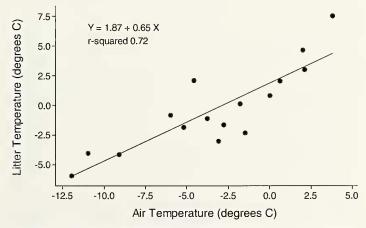


Figure 2.—Linear regression of ambient air vs. plant litter temperature (° C) in north-central Illinois, USA.

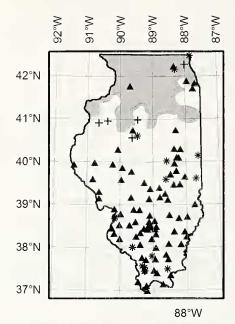


Figure 3.—Brown recluse spider records and estimated mean January litter temperature at or below the long-term minimum LD $_{100}$ of -5° C indicated by shading for Illinois. Triangles denote records with voucher specimens from the Illinois Natural History Survey (INHS), other museums, and specimens submitted to the principal author's Bi-State Brown Recluse Project and to R. Vetter (2005 and personal communication). Asterisks are records of spiders without voucher specimens but recorded by arachnologists at the INHS. Crosses indicate known or probable human transport of spiders from within the known range of the brown recluse via two main routes: warehouses with daily shipments of materials or one-time transport to a residential area by moving stored materials.

author's Bi-State Brown Recluse Project (with collaboration from Rick Vetter, Univ. of California-Riverside), the Illinois Natural History Survey (INHS) and other museum sources, and records of Joe Beatty kept at the INHS (Fig. 3). Brown recluses are recorded primarily in the area of the state south of the -5° C litter temperature isotherm that correlates with the species long-term LT₁₀₀. At least five of the outlying records north of this isotherm (e.g., Chicago area, other north-central Illinois sites) are known to be due to transport by commerce or movement of stored household items from southern portions of USA well within the established distribution of the species.

DISCUSSION

With public concern over brown recluse bites elevated by dramatic photos and dubious stories on the internet, public perception that the spider occurs throughout the United States is widespread yet unfounded (Vetter 2005). Anecdotally, concerns about the northward movement of organisms due to global warming also contributes to exaggerated fears of the threat from a brown recluse bite far north of its usual range. Our study suggests that, given its cold temperature tolerance, the brown recluse is unlikely to become established north of its range in the wild.

The brown recluse has an LD₅₀ of -9° C for 4-h exposures similar to those found by Fischer & Vasconcellos-Neto (2003) for the South American species *Loxosceles intermedia* and *L. laeta* whose LD₅₀ is -7° C for shorter 1-h exposures. The brown recluse may be more tolerant of somewhat colder

temperatures but the similarities are notable given the substantially different latitudes occupied by these three species (38°N for *L. reclusa* used in this study, and 24°S for *L. intermedia* and *L. laeta* from southern Brazil). Although Kirchner (1987) reported wide variability in supercooling points not only within genera but even within some species, based on these limited tests, the genus *Loxosceles* in the Americas may have relatively inflexible limits with respect to cold temperature tolerance.

Several limitations must be considered when extrapolating our lab data to field conditions. First, the rate of temperature change in the lab may be more rapid than what spiders are exposed to in the wild. Although our lab populations were dropped at a rate of 2° C/h, previous studies of lower critical temperatures in spiders have varied widely. Almquist (1970) acclimated various species at 4° C and then lowered temperatures by a more gradual 1° C/h. However, in studies on thomisids (Schmalhofer 1999) and Loxosceles (Fischer and Vasconcellos-Neto 2003) temperatures were lowered from room temperature to test temperatures at far faster rates than in our study (12 and 30° C/h, respectively). Which of these is a more accurate representation of the field situation is difficult to determine. In our study, litter temperatures dropped as much as 3° C/h even late in the fall (November). In the fall in Illinois, it is not uncommon for temperatures to drop more than 10° C in 1 h as a major cold front passes through an area (University of Illinois 2007). Although spiders may be exposed to very rapid temperature change, they may enter diapause before such temperature fluctuations occur by responding instead to changing photoperiods and avoiding the need for a sudden physiological response to rapidly dropping temperatures.

Second, because temperatures fluctuate among and within days over winter, the continuous exposure in our long-term laboratory tests may be more severe than actual conditions in the field that we represented by the isotherms of mean low January temperatures (Fig. 3). Such daily fluctuations above average minimum temperatures may be important to survival.

Third, the relatively low humidity we maintained in the incubators is probably also harsher than that experienced in overwintering microhabitats. However, *L. reclusa* is very tolerant of water loss and persists indefinitely in the lab with no access to water. Eskañ et al. (1977) report extremely low rates of water loss in brown recluses, the lowest of any spiders tested to that date.

Finally, extreme minimum temperatures might also be expected to increase brown recluse mortality and therefore limit brown recluse distribution. However, the mildest extreme low temperatures recorded in Illinois over the past 30 yr was -26° C in the southernmost portion of the state, a temperature that far exceeds the minimum short-term tolerance of *L. reclusa* in the lab. Yet brown recluses are common throughout southern Illinois. This suggests that at least some spiders must inhabit hibernacula sufficiently insulated to protect themselves from extreme lows for periods of several days.

We have shown a crude correlation of winter temperature with brown recluse temperature tolerance and distribution in Illinois but certainly other abiotic and biotic factors are limiting, especially in other portions of its range. For instance,

the brown recluse does not occur in most of Florida and the Atlantic coast where temperatures are mild enough for overwinter survival. Similarly, other factors must be in play limiting its westward expansion across the Great Plains. As a final caveat, much more needs to be known about the distribution of L. reclusa in natural habitats vs. buildings. Most records of brown recluses are of specimens collected in climate-controlled buildings, a factor that confounds attempts to relate ambient temperature to distribution. Where brown recluse records are more common and household infestation is not unusual we can infer that healthy wild recluse populations are probably a source of immigrants, and therefore must be adapted to ambient temperatures. However, records of brown recluses on the margin or outside of their normal range are often from buildings. It is rarely explored if wild populations exist in the immediate area of such records and these populations may only persist indoors in climate-controlled settings. Future collectors may wish to document more precisely the synanthropic distribution of brown recluses compared to their occurrence in natural habitats.

ACKNOWLEDGMENTS

The authors acknowledge the Monmouth College Biology department for financial support for equipment purchases. Peter Eilers of Willamette University (Salem, OR) and Charles Ehlschlaeger of Western Illinois University (Macomb, IL) provided invaluable assistance producing the map of recluse distributions and litter isotherms. Jack Bowles and colleagues at Little Creek Nature Preserve in Florissant, Missouri granted permission to collect. Kiel Krause helped maintain the spiders and assisted with one critical experiment. The principal author thanks the Associated Colleges of the Midwest for financial support through the Faculty Career Enhancement (FaCE) grant. Thanks to Greta Binford and Lewis and Clark College (Portland, OR) for providing lab and office space and time to write during the principal author's sabbatical. Finally, thanks to Rick Vetter for inspiring this work through his own obsession with brown recluse spider distribution.

LITERATURE CITED

- Aitehison, C.W. 1978. Spiders active under snow in southern Canada. Symposium Zoological Society of London 42:139–148.
- Almquist, S. 1970. Thermal tolerances and preferences of some duneliving spiders. Oikos 21:230–236.
- Eskafi, F.M., J.L. Frazier, R.R. Hocking & B.R. Norment. 1977. Influence of environmental factors on longevity of the brown recluse spider. Journal of Medical Entomology 14:221–228.
- Fischer, M.L. & J. Vasconcellos-Neto. 2003. Determination of the maximum and minimum lethal temperatures (LT₅₀) for *Loxosceles intermedia* Mello-Leitão, 1934 and *L. laeta* (Nicolet, 1849) (Araneae, Sicariidae). Journal of Thermal Biology, 563–570.
- Gertsch, W.J. & F. Ennik. 1983. The spider genus *Loxosceles* in North America, Central America, and the West Indies (Araneae, Loxoscelidae). Bulletin of the American Museum of Natural History 175:264–360.
- Hite, J.M., W.J. Gladney, J.L. Lancaster, Jr. & W.H. Whitcomb. 1966. Biology of the brown recluse spider. Arkansas Experiment Station Bulletin 711:3–26.
- Husby, J.A. & K.E. Zachariassen. 1980. Antifreeze agents in the body fluid of winter active insects and spiders. Experientia 36:963–964.
- Illinois State Climatologist Office. 2006. Illinois Climate Summaries, mean low temperatures, January, 1971–2000. Online at: http://www.sws.uiuc.edu/atmos/statecli/Summary/Illinois.htm.
- Kirchner, W. 1987. Behavioral and physiological adaptations to cold. Pp. 66–77. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, New York.
- McDaniel, I.N. & D.T. Jennings. 1983. Loxosceles reclusa (Araneae: Loxoscelidae) found in Maine, USA. Journal of Medical Entomology 20:316–317.
- Schmalhofer, V.R. 1999. Thermal toleranees and preferences of the crab spiders *Misumenops asperatus* and *Misumenoides formosipes* (Araneae, Thomisidae). Journal of Arachnology 27:470–480.
- University of Illinois. 2007. WW2010. Online Guide, "Cold Fronts." http://ww2010.atmos.uiuc.edu/(Gh)/home.rxml.
- Vetter, R.S. 2005. Arachnids submitted as suspected brown recluse spiders (Araneae: Sicariidae): Loxosceles spiders are virtually restricted to their known distributions but are perceived to exist throughout the United States. Journal of Medical Entomology 42:512–521.
- Zachariassen, K.E. 1985. Physiology of cold tolerance in insects. Physiological Reviews 65:799–832.